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Leptonycteris nivalis.

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Leptonycteris (Lydekker, 1891)

Ischnoglossa Saussure, 1860:491. Type species *Ischnoglossa nivalis* Saussure (preoccupied by *Ischnoglossa* Kraatz, 1856, a beetle).

Leptonycteris Lydekker, 1891:674, *in* Flower and Lydekker (1891). Type species *Ischnoglossa nivalis* Saussure, 1860.

CONTEXT AND CONTENT. Order Chiroptera, Family Phyllostomidae, Subfamily Glossophaginae. The genus *Leptonycteris* contains three species: *L. nivalis*, *L. yerbabuenae* (=*L. sanborni*), and *L. curasoae* (Hall, 1981; Honacki et al., 1982). The following key to species was developed from diagnostic features reported by Davis and Carter (1962) and Hoffmeister (1957):

1 Three phalanges of third finger longer than third metacarpal; length of forearm usually 55 mm or greater, averaging 57 mm; fur long and lax; uropatagium moderately hairy with a conspicuous fringe of hairs 3 to 4 mm long ..... *L. nivalis*

Three phalanges of third finger of equal or lesser length than third metacarpal; length of forearm usually 55 mm or less, averaging about 54 mm; fur short and dense; uropatagium sparsely haired to naked with fringe of hairs inconspicuous to absent 2

2 (1) Length of upper toothrow (from canine to last molar) greater than or equal to 9 mm; upper and lower teeth, especially incisors and premolars, larger and evenly spaced; uropatagium sparsely haired and with a slight fringe ..... *L. curasoae*

Length of upper toothrow (from canine to last molar) usually less than 9 mm; upper and lower teeth, especially incisors and premolars, smaller and less evenly spaced; upper incisors in two pairs separated by a median gap; uropatagium nearly naked..... *L. yerbabuenae*

Leptonycteris nivalis (Saussure, 1860)

Big Long-nosed Bat

Ischnoglossa nivalis Saussure, 1860:491. Type locality "near snow line of Mt. Orizaba, Veracruz."

Leptonycteris nivalis: Miller, 1900:126.

Leptonycteris nivalis longala Stains, 1957:355. Type from "12 mi. S and 2 mi. E Arteaga, 7500 ft., Coahuila."

CONTEXT AND CONTENT. Context noted in generic summary. Subspecies are not currently recognized.

DIAGNOSIS. *Leptonycteris* species resemble those of the genus *Lichonycteris* in that both lack third molars, but *Leptonycteris* normally has lower incisors while *Lichonycteris* has none (Hall, 1981). A specimen of *Leptonycteris nivalis* that has lost its lower incisors can be distinguished from *Lichonycteris* by the spacing of the upper incisors between the canines: upper incisors of *Lichonycteris* are evenly and widely spaced while those of *Leptonycteris* form an almost continuous line with the only notable space (if present) being at the midline (Hall, 1981). *Choeronycteris mexicana* can be distinguished by its protruding, short tail (Barbour and Davis, 1969).

Compared to *L. yerbabuenae*, *L. nivalis* has longer (7 to 8 mm on dorsum) fluffier pelage (Davis and Carter, 1962), is larger in several cranial and external measurements (Davis and Carter, 1962), has a shorter presphenoid ridge and has deeper, and more pronounced basisphenoidal pits (Watkins et al., 1972). *L. nivalis* has a longer (>105 mm) third finger, with the sum of the lengths of the three phalanges of the third finger averaging greater than the length of the third metacarpal (Barbour and Davis, 1969; Hoffmeister, 1957). *L. nivalis* has a longer (10% or more) head and body (Hoffmeister, 1957), and has pelage that is less red and more drab than *L. yerbabuenae* (Hoffmeister, 1957). Compared to *L. curasoae*, *L. nivalis* has a lighter pelage and the interfemoral membrane is broader and more hairy (Miller, 1900). The upper incisors are not as equally spaced.

GENERAL CHARACTERS. *Leptonycteris nivalis* is a large glossophagine bat (Phillips, 1971; Fig. 1). The slender skull has complete zygomata (Hall, 1981; Fig. 2). The muzzle is greatly lengthened, but less so than in some other glossophagines (Hoffmeister, 1957). *Leptonycteris* is characterized by elongated molars with a faint W-shaped pattern (Hall, 1981). The dental formula is i 2/2, c 1/1, p 2/3, m 2/2, total 30 (Davis, 1974). External characters of the big long-nosed bat include a reduced (4 mm or shorter), moderately hairy uropatagium with a hairy 3 to 4 mm fringe (Davis and Carter, 1962); a triangular erect noseleaf (Barbour and Davis, 1969); a very long extensile tongue tipped with long hairlike papillae (Greenbaum and Phillips, 1974); and short ears (Davis, 1974). Although external observation suggests that *L. nivalis* lacks a tail, a very short concealed tail consisting of three vertebrae is present (Hoffmeister, 1957).

Leptonycteris nivalis has a sooty or drab brown color (Barbour and Davis, 1969) and is darker on the posterior dorsum and paler ventrally and on the anterior dorsum (Hall, 1981). Hairs are white at the base and silvery at the tips (Davis, 1974).

Means for three external measurements (in mm) are: total length, 83; length of foot, 17; and length of ear from notch, 15 (Davis, 1974). Means and extremes of cranial measurements (in mm) for three adult males followed in parentheses by those for seven adult females from Texas and Mexico are (Davis and Carter, 1962): condylobasal length, 27.1, 26.5 to 28.0 (27.2, 26.2 to 28.3); zygomatic breadth, 11.4, 10.7 to 12.0 (11.3, 10.9 to 11.6); interorbital width, 5.3, 5.3 to 5.4 (5.1, 4.3 to 5.4); mastoidal breadth, 12.0, 11.5 to 12.5 (11.8, 11.5 to 12.0); length of palate from alveolus, 14.5, 14.0 to 15.0 (14.5, 13.3 to 15.3); maxillary toothrow, 9.2, 8.9 to 9.6 (9.2, 8.5 to 9.5); length of mandible 19.2, 18.5 to 19.7 (19.1, 18.2 to 20.3). Means for two other cranial measurements (in mm) for six males and eight females from Chisos Mountains, Brewster Co., Texas, are (Hoffmeister, 1957): greatest length of skull, 28.1, and width of braincase, 10.7. Mandibular

FIG. 1. Side view of facial region of *Leptonycteris nivalis* showing long protrusile tongue and bat fly ventral to eye. Specimen, from Big Bend National Park, Texas, photographed in 1967 by D. A. Easterla.

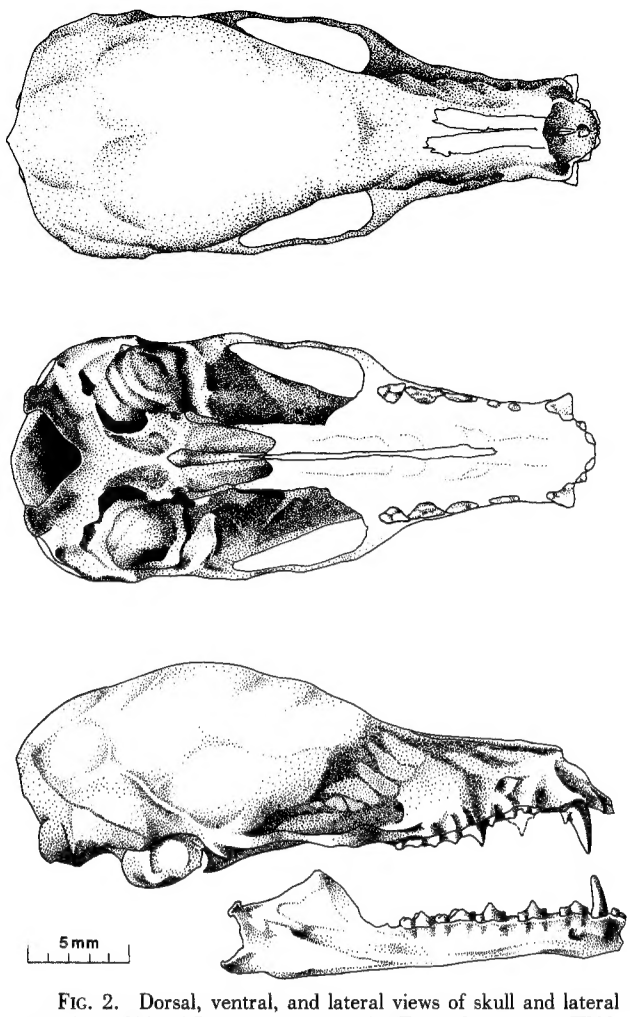

FIG. 2. Dorsal, ventral, and lateral views of skull and lateral view of mandible of *Leptonycteris nivalis* (Texas Cooperative Wildlife Collection 3556, female) from Chisos Mountains, Brewster Co., Texas. Drawings by M. A. Thomas.

depth behind the last molar is 2.0 to 2.5 mm deeper in males than in females; no other marked sexual dimorphism was found for cranial features (Davis and Carter, 1962).

Means and extremes (in mm) for postcranial measurements from three adult males followed in parentheses by those for seven adult females, respectively, from Texas and Mexico (Davis and Carter, 1962) are: length of forearm, 57.2, 55.4 to 59.5 (56.6, 54.5 to 58.2); length of third metacarpal, 50.1, 49.0 to 51.7 (50.3, 49.0 to 51.5); length of third finger, 110.4, 107.1 to 115.3 (110.0, 108.4 to 112.3); length of terminal phalanx of third finger, 17.6, 16.2 to 18.7 (17.9, 17.0 to 18.3). De la Torre (1955) observed a size cline in *L. nivalis* such that individuals from the northern portion of the range of the species are larger than those from the south. Average body mass is 24 g (Davis, 1974).

DISTRIBUTION. *Leptonycteris nivalis* is known from southern Trans-Pecos Texas southward through central and eastern Mexico, mostly east of the 102° meridian and south at least to Guerrero and Guatemala (Hoffmeister, 1957; Fig. 3). Specimens in the United States have been collected from the Chisos Mountains, Big Bend National Park, Brewster Co., Texas (Borell and Bryant, 1942); and Chinati Mountains, Presidio Co., Texas (Mollhagen, 1973). Although Jones and Findley (1963) reported *L. nivalis* from the Peloncillo Mountains and Guadalupe Canyon of Hidalgo Co., New Mexico, Findley et al. (1975) did not list this species as occurring in New Mexico. Rather, long-nosed bats from Hidalgo Co. are identified as *L. yerbabuenae*. Peripheral collection records not included in Hall (1981) are: Sinaloa: 10.3 mi (16.6 km) W by road of Palmito, 183 m (Baker and Cockrum, 1966); Tamaulipas: 6.5 mi (10.4 km) N, 13.1 mi (21 km) W Jimenez (Baker and Cockrum, 1966); Nuevo

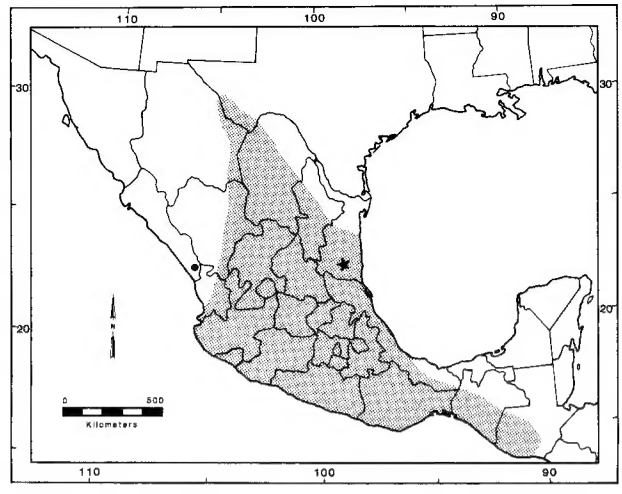

FIG. 3. Distribution of *Leptonycteris nivalis* modified from Hall (1981). Dot indicates extralimital record in Sinaloa, Mexico. Star denotes locality for only known fossil, Cueva de Abra, Tamaulipas, Mexico.

Leon: Cerro Potosi near La Joha, 3,503 m (Koestner, 1941). *L. nivalis* is rare throughout its range (Barbour and Davis, 1969).

FOSSIL RECORD. Late Pleistocene material of *L. nivalis* has been reported from a travertine ledge in a cave, Cueva de Abra, in tropical southern Tamaulipas, Mexico (Dalquest and Roth, 1970; Fig. 3). The material from this site is a lower jaw without teeth.

FORM AND FUNCTION. *Leptonycteris nivalis* possesses as many as 22 deciduous teeth: i 2/1, c 1/1, p 2-3/2-3 (Phillips, 1971). Variability in the deciduous premolar count probably results from the small size of the teeth, their early loss, or their reabsorption before birth. The first upper premolars are not replaced by permanent teeth. The first lower premolar is the first permanent tooth to erupt; it is followed by the coincidental eruption of the first upper and lower molars and the outer lower incisors. The first and second upper premolars and the upper canines and incisors reach the functional eruptive phase at about the same time. These upper teeth and the second and third lower premolars erupt simultaneously. The second upper and lower molars are the last permanent cheekteeth to reach the occlusal plane and they erupt at the same time as the lower canines. The lower inner-incisors are the last permanent teeth to develop (Phillips, 1971). Agenesis of the cheekteeth is uncommon in *L. nivalis*, but an adult male had a congenitally-missing upper molar. In both sexes, lower inner-incisors often fail to develop. Occasionally, males congenitally lack the second lower incisors. *L. nivalis* has a fairly high incidence of first upper premolar loss due to infestations by oral mites (Macronyssidae). Additionally, incisors frequently are lost, but the remaining lower teeth, except the lower first and second molars, rarely are lost (Phillips, 1971).

The highly protrusile tongue of *L. nivalis*, an adaptation for its diet of nectar and pollen, attaches to the posterior sternum (Wille, 1954) and can be extended beyond the tip of the rostrum for distances as great as the length of the head (Winkelmann, 1971). Dorsoventrally-oriented rows of hairlike papillae cover the anterolateral surfaces near the tip of the tongue; a median trough, which is narrowest distally, lies between these fields of hairlike papillae (Greenbaum and Phillips, 1974). Most of the median trough is covered by small, bifid, compact, mechanical papillae except for a restricted cluster of small, horny papillae surrounding a pair of large, bifid, horny papillae located about 7 mm behind the tip of the tongue. Keratinization of tongue epithelium is greatest in the vicinity of these horny papillae. A midline posterior groove extends from the rear of the median trough towards the base of the tongue. Numerous singly-pointed, posteriorly-directed filiform papillae lie flat against the dorsal and lateral surfaces of this basal section of the tongue (Greenbaum and Phillips, 1974). In *L. sanborni*, papillae in the corresponding region have a different morphology and deployment: the papillae have hooked ends and are lifted off of the tongue surface. There is a correlation of hooked papillae morphology with the absence of mite infestations of the gingivae in *L. sanborni*. Mite infestations in

L. nivalis may persist because hookless, appressed papillae cannot rake mites from the gums as the tongue retracts. Three other types of papillae (fungiform, medial vallate, and lateral vallate) occur in restricted regions of the basal half of the tongue of *L. nivalis* (Greenbaum and Phillips, 1974). Longitudinal grooves running about half the length of the tongue on each side were reported by Wille (1954), but were not detected in other studies (Greenbaum and Phillips, 1974; Park and Hall, 1951; Winkelmann, 1971).

Most of the mass of the tongue in *L. nivalis* is composed of muscle tissue arranged in horizontal, vertical, and longitudinal bundles (Greenbaum and Phillips, 1974). Vascularization of the tongue is via a lingual artery in the midline flanked by paired lingual ligaments and lingual veins. Glands of von Ebner, associated with circumvallate papillae, and mucus glands are located in the posterodorsal area of the tongue. The majority of the elastic fibers in the tongue are located in the lamina propria of the dorsal and ventral surfaces and of the hairlike papillae (Greenbaum and Phillips, 1974).

Leptonycteris nivalis is an agile flyer, capable of quick maneuvering and relatively high speed flight (Hayward and Davis, 1964). In speed trials, one female *L. nivalis* flew 30.5 m in 8.0 s and another female required 13.6 s. Hayward and Davis (1964) attributed the slightly lower than expected speed of *L. nivalis* to the need to hover at blossoms for feeding. *L. nivalis* makes swooshing sounds as it flies and can fly straight up while maintaining a horizontal body position (Barbour and Davis, 1969).

Although *L. nivalis* lives in an arid environment, it has a much lower than expected kidney-medulla-thickness to cortex-thickness ratio and produces a dilute urine with low maximal concentrations. This is due to the diet of low protein, high-water foods (Kunz, 1982). *Leptonycteris* appears to relax its degree of thermoregulation in the middle range of ambient temperatures, but maintains body heat at both high and low ambient temperatures (Yalden and Morris, 1975).

ONTOGENY AND REPRODUCTION. Normal litter size is one (Davis, 1974). The breeding season in Texas appears to be restricted to April, May, and June (Davis, 1974). Easterla (1972) reported finding no direct evidence of parturition by *L. nivalis* in the cave on Emory Peak, but did find lactating females there in June and July and first noted flying juveniles on 27 June (Easterla, 1973). Easterla (1972) and Schmidly (1977) believe that the young are born in Mexico prior to the arrival of the adult females in this cave. By July the young are half-grown (Davis, 1974). Barbour and Davis (1969) caught an almost full-grown *L. nivalis* on 5 July that probably had been born in late May or early June.

ECOLOGY. Barbour and Davis (1969:36) report the favored habitat of *L. nivalis* as the high-elevation pine-oak country (pinyon pine, *Pinus cembroides*; drooping juniper, *Juniperus flaccida*; redberry juniper, *J. pinchoti*; gray oak, *Quercus grisea*; Emory oak, *Quercus emory*; Grave's oak, *Q. gravesei*) from about 1,524 m in elevation up to snowline (Easterla, 1972). However, collection sites much lower than this (762, 701, and 567 m) in agave (*Agave chisosensis*, no common name in use; *A. scabra*, havard agave; and *A. lechuguilla*, lechuguilla) and desert-scrub woodlands have been reported (Easterla, 1972). Koestner (1941) found a colony of 10,000 at an elevation of 3,505 m at Cerro Potosi near La Joha, Nuevo Leon.

This species is a colonial cave dweller which usually inhabits deep caverns but can also be found in mines, culverts, hollow trees, and unused buildings (Barbour and Davis, 1969; Davis, 1974; Hoffmeister, 1957; Kunz, 1982; Nowak and Paradiso, 1983; Schmidly, 1977). The only known colony in the United States occupies a cave at Emory Peak in the Chisos Mountains, Brewster Co., Texas, at 2,286 m (Barbour and Davis, 1969). Davis (1974) described the cave in Emory Peak as having considerably cooler air inside than outside of the cave during summer and a breeze blowing through at all times. Caves inhabited by *L. nivalis* can be recognized by a musty smell similar to that of *Tadarida brasiliensis* (Barbour and Davis, 1969). The floor and walls of the *L. nivalis* roost in the Emory Peak cave are slick and covered with yellowish, sweet-odored, semi-liquid droppings (Easterla, 1972, 1973). Colony size in this cave ranged from as high as 10,650 bats in 1967 to as low as zero bats in 1970 (Easterla, 1972). An explanation for these drastic fluctuations is that this cave serves as a northern "spillover" colony during years of high populations or low food supply in Mexico (Easterla, 1972). *L. nivalis* clusters in densities of about 1,615 bats/m^2 (Easterla, 1972). The bats hang from the ceiling with adults and half-grown juveniles intermixed (Davis, 1974).

Apparently, adult males segregate geographically from the females in the summer and do not occupy the northern part of the species' range (Dalquest and Walton, 1970; Davis, 1974; Easterla, 1972; Schmidly, 1977). Easterla (1972) caught only three males in five years of study in Big Bend National Park, Texas.

Leptonycteris nivalis has been known to share caves with *Plecotus townsendii* (Barbour and Davis, 1969; Davis, 1974; Easterla, 1972). *Myotis thysanodes* and *M. volans* have been found in roosts used by *L. nivalis*, but not when *L. nivalis* was present (Easterla, 1973).

Leptonycteris nivalis must make long migrations to ensure an adequate supply of its limited diet (Humphrey and Bonaccorso, 1979). Migration is necessary also because *L. nivalis* does not hibernate (Schober, 1984). Evidently, the onset of the rainy season and cold weather initiates migration (Easterla, 1973). In the summer, *L. nivalis* occurs at higher elevations in Big Bend National Park, Texas, and at a few locations in northern Mexico; to winter it migrates farther south in Mexico, at least as far as Jalisco and Morelos (Barbour and Davis, 1969; Kunz, 1982; Schmidly, 1977). In the very southern part of its range, *L. nivalis* intergrades with *L. yerbabuenae* (Baker and Cockrum, 1966; Davis and Carter, 1962; Hoffmeister, 1957).

Leptonycteris nivalis emerges relatively late in the evening to feed (Barbour and Davis, 1969). *L. nivalis* is a primary consumer that feeds on nectar, pollen, insects and probably soft, succulent cactus fruits during the non-flowering season (Allen, 1940; Barbour and Davis, 1969; Hoffmeister, 1957). Insects are probably picked up accidentally as the bat gathers nectar and pollen from flowers (Hoffmeister, 1957), but Rasweiler (1977) indicated that insect ingestion might be nutritionally significant. In the Chisos Mountains, this bat feeds from flowers of *Agave scabra* and *A. chisosensis*, but at lower elevations, another food plant might be *Agave lechuguilla* (Easterla, 1972). Cockrum and Hayward (1962) reported Schott agave (*Agave schotti*) and saguaro cactus (*Carnegia gigantea*) as food sources for *L. nivalis*; this study was done in Arizona and probably refers to *L. sanborni* rather than *L. nivalis* as currently recognized. Jimson weed (*Datura stramonium*), wax mallow (*Malvaviscus*), mescal (*Agave* sp.), and various cactus flowers also serve as food for the bat (Barbour and Davis, 1969; Davis, 1974; Schmidly, 1977; Schober, 1984). Duges (1906; in Allen, 1940) described a specimen from Guanajuato, Mexico, whose stomach was filled with pollen from the white-flowered *Malvaviscus acerifolius*. In 1944, Davis (1974) captured an adult male which ate the pollen and nectar of an *Agave scabra* plant. When eating from *Agave*, *L. nivalis* crawls down the stalk, thrusts its snout into the flowers, and licks nectar from them with its long tongue which can be extended to a length of 76 mm and can reach nectar at the base of the flower corolla; *L. nivalis* emerges from these flowers covered with pollen (Barbour and Davis, 1969; Cockrum and Hayward, 1962; Faegri and Van der Pijl, 1979; Wille, 1954). *L. nivalis* is an effective pollinator of many of the cacti, agave, and perhaps other plants on which it feeds (Davis, 1974; Faegri and Van der Pijl, 1979).

Oral infestations by mites (Macronyssidae: *Radfordiella oricola*) are a primary etiological factor in destruction of periodontal tissues (Phillips, 1971). Infestation by the mites may be related to the diet of nectar, pollen, and soft fruits (Phillips et al., 1969). These mites reside between the gingiva and lingual surface of the roots of the teeth (Phillips et al., 1969). The general effect of these oral mites resembles typical periodontitis; the palatal lesions usually are found on the lingual side of the upper premolars and molars and cause resorption of bone of the hard palate, destruction of periodontal ligaments, resorption of cementum and dentin, and loss of teeth (Phillips, 1971). *L. yerbabuenae* has no such lesions even when found in the same cave as *L. nivalis* (Phillips et al., 1969). Examination of 111 skulls of *L. nivalis* from Texas, Nuevo Leon, Coahuila, Michoacán, Jalisco, Hidalgo, Guerrero, México, and Morelos revealed all adults (except four of 14 specimens from Texas) to have palatal lesions (Phillips, 1971; Phillips et al., 1969).

Six species of ectoparasites have been reported from *L. nivalis*; *Periglischrus vargasi* (Spintunicadae), *Myodopsylla gentilis* (Ischnopsyllidae), *Sternopsylla texana* (Ischnopsyllidae), *Basilia corynorhini* (Nycteribiidae), *Trichobius sphaeronotus* (Streblidae), and *Nycteriglyphus texanus* (Rosensteiniidae; O'Connor et al., 1977; Whitaker and Easterla, 1975). *N. texanus* is a tiny yellow mite found in large numbers crawling on the cave walls and in guano, but not on the body of *L. nivalis* (Whitaker and Easterla, 1975). Villa and Jimenez (1961) reported the presence of rabies virus in a

specimen of *L. nivalis* collected in Cueva del Canon del Zopilote, 12.5 km S Mexicala, Guerrero, Mexico.

REMARKS. Davis and Carter (1962) determined the genus *Leptonycteris* to have three species: *L. curasoae*, *L. sanborni*, and *L. nivalis*. Davis and Carter (1962) considered *L. yerbabuenae* to be a synonym for *L. nivalis*. Hall (1981) agreed with the contention of Ramierez-Pulido and Alvarez (1972) that *L. yerbabuenae* is not a synonym for *L. nivalis* but is instead the proper name for *L. sanborni*.

Leptonycteris nivalis is known by several common names: big long-nosed bat, Mexican long-nosed bat, Mexican long-tongued bat, and nectar bat (Barbour and Davis, 1969; Hall, 1981). *Leptonycteris* derives from the Greek *leptos* meaning slender and *nycteris* meaning bat, and probably refers to the long, slender skull, rostrum, and tongue of this genus. The specific epithet *nivalis* stems from *nivis* meaning snow and probably refers to the type specimen which was found at the snowline of Mt. Orizaba.

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